HORMONES AND SHIFTING ECOLOGY THROUGHOUT PLANT DEVELOPMENT

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Abstract. Hormones modulate complex suites of ecologically relevant behaviors through interactive cascades of signal transduction; evolutionary changes in the function of a single hormone can result in multiple changes in plant traits. Sites of hormone action and tissue sensitivity change throughout plant ontogeny, as embryos, seedlings, and reproductively mature plants cope with shifting suites of environmental variables and resource availability. Phenotypic plasticity and correlations and trade-offs between life history traits (such as resource use efficiency and allocation to growth and differentiation of meristems) also change as plants age; hormonal changes are central to these shifts. I synthesize evidence from the molecular and physiology literature and present novel data on mangrove propagules, seedlings, saplings, and trees. Together, these data demonstrate that several ecologically important traits are hormonally mediated (both in the short term and over evolutionary time) in the diversification of plant lineages. I focus on two hormones with contrasting action: (1) abscisic acid (ABA), which regulates internal plant osmotic stability, membrane integrity, seed dormancy, and stomatal conductance; and (2) cytokinins (zeatin and allied adenine derivatives), which promote cell division, stimulate growth, delay leaf senescence, enhance the capacity of tissues to act as N sinks, and help to transduce signals of light and nutrient availability. ABA and cytokinin levels are correlated with patterns of osmotic tolerance, photosynthesis, growth, and leaf longevity, and their concentrations in specific tissues change throughout plant development. Ecologists and evolutionary biologists are in a strong position now to creatively comprehend, predict, and potentially engineer plant strategies and adaptive trade-offs over plant lifetimes in light of emerging knowledge of hormones.

Key words: abscisic acid; allocation; cytokinins; evolution; growth; mangroves; maturation; phenotypic plasticity; phytohormones; plants; seedlings; zeatin.

INTRODUCTION

Hormones run most of the important aspects of life, including the major processes that demand the attention of many ecologists: resource capture, growth, and sex. Physiological ecologists have long recognized the importance of hormones in integrating environmental signals, controlling flexible physiological responses, regulating phenotypic plasticity, conferring maternal effects, and constraining life history strategies. A decade ago, Feder and Block (1991) exhorted animal physiologists to join forces with molecular geneticists to study the evolution of hormonal physiology in an adaptive ecological context. They have risen to the charge. With the advent of new techniques for manipulating endogenous hormone levels in animals, increasingly elegant experiments have demonstrated the ways in which hormones coordinate complex suites of behaviors that are sensitive to strong natural selection (see recent reviews by Sinervo and Svensson [1998], Ketterson and Nolan [1999], and Dufty et al. [2002]). The emerging, integrative field of “eco-devo” (sensu Gilbert 2001), is beginning to flourish as our understanding of hormonal evolution and controls on development improves.

Meanwhile, plant physiologists have been busily untangling the means by which phytohormones function during plant morphogenesis and throughout life (Davies 1995). While it is true that plant and animal hormones function differently in terms of their production sites and action (well summarized by Weyers and Paterson [2001], Kushiro [2003]), hormones have much potential to explain major evolutionary innovations and novel traits in plants. Thus, the ecological and evolutionary significance of hormonal physiology in plants is becoming clearer as we come to understand signaling pathways, mechanisms of tissue sensitivity, genetic bases for hormonal action, and synergistic and antagonistic interactions among hormones. Recent comparative studies, for example, have shown that similar evolutionary changes in the function of a single hormone within multiple plant lineages can be manifested in convergent changes in multiple plant traits that may in part explain trade-offs and correlations among characters (e.g., Farnsworth 2000). Plants constitute excellent systems for studying “proximate” hormonal effects on physiology and fitness and “ultimate” impli-
cations for evolution of correlated traits. A wealth of well-characterized mutant lines with differing hormonal sensitivities and levels of production exist across a variety of species, and more are emerging all the time (McCourt 1999). The existence of rapid-cycling cultivars and annual species also permit studies of character change over several generations (e.g., Mitchell-Olds 2001). Ecologists are also moving beyond Arabidopsis, transcending the traditional crop and herbaceous study systems to investigate the hormonal physiology of plants growing in a variety of complex environmental situations (e.g., Voesenek and Blom 1996, Farnsworth and Farrant 1998, Mercier and Endres 1999, Wang et al. 2001, Zott et al. 2001).

Plant form, physiology, and sites of hormone action and tissue sensitivity also change throughout plant ontogeny, as plants cope with shifting suites of environmental variables and resource availability (Trewavas 1986, Evans and Poethig 1995, Amzallag 2001). Correlations and trade-offs between life history traits (such as resource use efficiency and allocation to growth and differentiation of meristems) also change as plants age. Hormonal changes are central to these shifts, but mechanisms are only now becoming clearer. These mechanisms are likely to involve an interplay of complex signal transduction pathways, secondary messengers, differential synthesis and sensitivity of receptors, relative control by hormones and extrinsic factors, and variable phenotypic expression of hormone effects (Paterson et al. 2001, Weyers and Paterson 2001). While both ecologists and physiologists recognize that growing plants are dynamic systems, ecologically relevant traits and hormone action have rarely been studied in an explicitly dynamic developmental context, spanning the course of development from embryo to tree.

Here, then, is an opportunity to understand plant ecology more fully by integrating among approaches from evolutionary, molecular, and developmental biology. Predicting variability in plant responses over time, measuring fitness costs of phenotypic plasticity, evaluating which life history phases are most vulnerable to stress, and scaling estimates of plant productivity from leaf to forest all depend on a stronger understanding of physiological controls on development. Here, I explore some linkages among suites of traits that change over ontogeny and that are known to be controlled at least in part by changing hormonal action. I will focus on two illustrative phytohormones with contrasting action: abscisic acid (ABA) and cytokinins, using examples from the literature and new data from studies of mangroves. Mangroves (a term applied to over 50 species in 15 families of woody halophytes restricted to tropical saline coasts, sensu Tomlinson [1994]) are a promising group in which to study convergent evolution of hormonal mechanisms involved in the maintenance of specialized traits (such as salt tolerance, viviparous reproduction, photosynthetic acclimation, etc.) that enable existence in challenging environments.

**Major life history transitions in plants**

Plants undergo recognizable ontogenetic phase shifts, which take the general trajectory of (1) rapid growth and tissue differentiation immediately following germination; (2) exponential growth to an asymptotic maximum size; (3) stabilization of woody support structures; (4) maturation and attainment of reproductive competence; and (5) senescence (Jones 1999). Studies have elucidated the physiological changes that can occur within a single growing leaf (e.g., Wait et al. 1998) or branch (Emery et al. 1998). However, the notion of whole-plant developmental stages and their corresponding physiological states have not often been integrated conceptually into long-term ecological studies of plants. With some exceptions (e.g., Honkanen and Haukioja 1998, Kearsley and Whitham 1998, Karban and Thaler 1999), most investigations of linkages among plant traits and plastic responses to the environment focus on plants at a single developmental phase, or measure growth variables (e.g., relative growth rate, net assimilation rate) that integrate across growth phases during a single season. Laboratory, greenhouse, and shadehouse studies of long-lived plants focus on more tractable seedlings or potted shoots. Herbaceous species tracked in the laboratory and field tend to be measured at reproductive maturity. Likewise, many comparative field studies of correlated traits focus only on mature plants, saplings, or small understory trees. Observations across plant lifetimes would afford insights into the origins of correlations among traits and selective pressures maintaining these correlations. McConnaughay and Coleman (1999) pointed out that observed changes in traits over time or between experimental treatments can arise from “ontogenetic drift” (sensu Evans 1972) as much as from extrinsic factors. That is, when allometric relationships among traits vary non-isometrically as plants grow, such patterns will change with plant age regardless of environmental conditions. Thus, they caution that ecologists consider ontogenetic drift when making static comparisons among populations.

Studies tracking herbaceous plants from seedlings to senescence have demonstrated that rates of photosynthesis, patterns of biomass allocation, relative growth rates, construction costs, leaf longevity, root : shoot ratios, plant architecture, levels of plasticity, and sensitivity to stress covary with plant age, and have reported varying levels of ontogenetic drift (Poorter and Pothmann 1992, Coleman et al. 1994, Romero and Marañon 1996, Lyons and Barnes 1998, Kikuzawa and Ackerly 1999, Harmens et al. 2000, Davies 2001). The few studies that have attempted to systematically compare juvenile, adult vegetative, and reproductively competent plants have demonstrated that ranges of juvenile traits can be decoupled from those of more mature
plants. For example, Clark and Clark’s (2001) long-term measurements of saplings of rainforest trees revealed few correlations between adult distribution and juvenile growth rates. Similarly, cotyledons and mature leaves, as well as juvenile and older shoots, differ in their resistance to herbivory (Kearsley and Whitham 1998, Karban and Thaler 1999).

Other studies have found higher levels of phenotypic flexibility, plasticity (sensu stricto), niche breadth across resource gradients, or responsiveness to environmental variables among younger woody plants than among older or reproductively mature plants and between lineages that differ in ontogenetic trajectory (Farnsworth and Ellison 1996, Pigliucci 1997, Eriksson 2002). This finding accords with an emerging hypothesis that early phenotypic plasticity may constrain plasticity later in life (Weinig and Delph 2001). To what degree are these adult differences due to changing extrinsic conditions vs. internal hormonal mechanisms?

Roles of phytohormones at different life stages

Extrinsic environmental signals trigger phase change in meristem cells of woody and herbaceous species, while intrinsic physiological cues regulate responsiveness to these signals as well as the length of time a meristem remains in a particular phase (Poethig 1990). Hormones may help plants control meristem identity as they track cumulative information about the distance of the apex from the roots and numbers of vascular branches (Kearsley and Whitham 1998, Jones 1999, Sachs 1999). Specific genes are implicated in the transformation of meristem identity, i.e., from vegetative to flowering (e.g., Weigel and Milsson 1995, Ratcliffe et al. 1999), but hormonal actions linked to these genes need to be elucidated fully. Several phytohormones play critical roles in maturation, biomass partitioning, growth, and stress responses of plants (Davies 1995). Among the best studied are abscisic acid (ABA) and cytokinins (zeatin [Z], zeatin riboside [ZR], isopentenyl adenine [IPA], and related molecules). These two phytohormones act independently and often oppositely on plant cells, exerting major influences plant development and growth.

**ABA, seeds to senescence.**—ABA is a low-molecular-weight acid that “modulates plant development, seed dormancy, germination, cell division, and cellular responses to environmental stresses such as drought, cold, salt, pathogen attack, and UV radiation” (Rock 2000:358). ABA also can inhibit cell elongation during responses to other stresses such as flooding (Hoffman-Benning and Kende 1992). Studies of both ABA-deficient and ABA-insensitive mutants indicate that ABA is a general “inhibitor” that slows metabolic processes and prepares plant cells for conservative stress avoidance (Chapin 1991, Leung and Giraudat 1998, McCourt 1999).

In the seed, ABA contributes to the upregulation of dehydrin proteins that act as membrane chaperones during the embryo desiccation that precedes dormancy (Ingram and Bartels 1996). ABA also suppresses germination-specific genes and counteracts the action of gibberellins that induce germination. ABA-deficient and insensitive mutants and seeds of naturally occurring plants that lack ABA exhibit high sensitivity to freezing and drying (recalcitrance), low dehydrin protein production, lack of dormancy, and, frequently, precocious germination (Box 1; Farrant et al. 1996, Farnsworth and Farrant 1998, Rock 2000). In the growing plant, ABA promotes stomatal closure by inducing ion efflux from guard cells to slow transpiration in response to drought, salinity, prolonged flooding, and other osmotic stress. It remains unclear whether ABA is itself a signal conveyed from the roots (which sense changes in soil osmoticum), or whether the hormone acts indirectly by stimulating gene transcription for proteins involved in a larger signal transduction pathway (Wilkinson and Davies 2002). However, it is clear that ABA is involved in short-term, plastic responses to changing water potential and nutrient availability, as ABA levels in drought-stressed tissues rise considerably within hours. Even tissues that do not normally produce ABA can be rapidly induced to produce the hormone or to release its activated (unconjugated) form from storage compartments (Box 1). Short-term boosts in ABA production in response to osmotic stress have been documented in mangroves (Box 1), *Suaeda maritima* (a halophyte) (Clipson et al. 1988), and *Iris hexagona* (a glycophyte) (Wang et al. 2001).

Interspecific differences in ABA levels suggest that plant populations subjected to strong selection under osmotic stress should exhibit microevolutionary differentiation in hormone production. Findings from mangroves growing in contrasting salinity environments show little such differentiation (Box 2). These findings point to a homeostatic mechanism in this species in which growing seeds (and viviparous propagules in mangroves) are shielded from varying external conditions. In contrast, Wang et al. (2001) found considerably higher levels of ABA in tissues of young *Iris hexagona* Walter seeds exposed to high salinity relative to a low-salinity population. Unlike the mangroves studied, however, this species produces dormant seeds. Differences in sensitivity to salinity declined with age of the seed, much as with *Rhizophora mangle*. *Impatiens capensis*, a non-halophyte, does show apparent population differentiation for abscisic acid responsiveness, as well as a trade-off between survivorship in saline conditions and reproductive output (Heschel and Hausmann 2001).

ABA production is compartmentalized among tissues. Although propagules of *Rhizophora mangle* and other viviparous mangroves exhibit low ABA levels throughout development, maternal pericarp and foliar tissues show significantly higher ABA concentrations, in line with those found for other salt-tolerant plants (Fig. 1). Wang et al. (2001) demonstrate similar com-
Box 1. Dynamics of ABA Levels in Developing Embryos of Viviparous and Nonviviparous Species

This study compared levels of the phytohormone abscisic acid in related groups of species that differ in terms of viviparity, and determined whether ABA production or release could be induced in viviparous mangrove propagules subjected to osmotic manipulation in the field. Nondormant, viviparous embryos ("propagules" sensu Tomlinson 1994) of 10 species across four disparate families of mangroves maintain unusually low levels of ABA throughout their development on the parent plant relative to their nonviviparous, upland relatives (Fig. 1). However, short-term increases in ABA levels can be induced by applied osmotic stress. Detached mangrove embryos of three different growth stages subjected to desiccation produce elevated levels of ABA relative to controls—levels comparable to related nonviviparous non-mangroves (Farnsworth and Farrant 1998). Increases in hormone levels can also be induced in situ on propagules that are still attached to mature trees. Four sets of 2–4-mo-old (7-cm long) embryos of the red mangrove, *Rhizophora mangle* L., on mature trees growing in ~20‰ salinity at the Fairchild Tropical Garden, Miami, Florida, USA, were selected. Ten propagules per set were randomly subjected to one of four treatments: (1) injection with 1 mL distilled water; (2) injection with 1 mL of 2% NaCl solution approximating measured embryo tissue concentrations of salt, serving as a solution control; (3) piercing needles without injection, serving as an injection control; and (4) comparably aged, unmanipulated controls. Propagules were collected 48 h following treatment and analyzed for ABA content by the methods of Farnsworth and Farrant (1998) and Weiler (1980). Mangrove propagules with osmoticum altered by freshwater injection produced ABA in concentrations three times higher than controls (Fig. 2), levels that are comparable to those found in embryos of nonviviparous non-mangroves and in maternal vegetative tissues (leaves and roots) of *Rhizophora mangle* (Fig. 1). These findings indicate that ABA is either produced in or translocated to embryonic tissues experiencing osmotic alteration, or that ABA is converted from a conjugated (inactive) to a free (metabolically active) form in response to this stress.

Box 2. Comparison of Baseline ABA Levels in Mangrove Propagules Growing in Contrasting Salinity Environments

While ABA levels can change rapidly in response to osmotic stress, ABA normally appears to remain at low concentrations in mangrove propagules growing in a range of salinities. A comparative study illustrated little differentiation among three populations of *Rhizophora mangle* L. growing in contrasting salinity conditions. I harvested six propagules from trees of each of (1) a hypersaline lagoon, West Pond, on Twin Cays, Belize (salinity of soil interstitial water measured with refractometer =51‰); (2) a tidally flushed, fringing mangrove stand on Wee Wee Cay (salinity =30‰); and (3) a riverine, mainland, mangrove stand along the Sitbee River (salinity =5–10‰). ABA concentrations were measured in tissues of three ages: (1) <30 d after pollination (dap); (2) 2–4 mo dap; and (3) >6 mo dap. ABA levels were highest among propagules from the hypersaline populations, especially in the youngest cohort of propagules (Fig. 3). However, ABA levels in older propagules converged among all sites, remaining low throughout ontogeny relative to concentrations in maternal tissues. The apparent lack of physiological differentiation among populations of *R. mangle* growing in different salinities may, in part, explain Smith and Snedaker’s (1995) finding that *R. mangle* seedlings from hypersaline and intermediate salinity sites did not differ in early growth rates—that is, that hypersaline propagules did not show higher acclimation or tolerance for salinity.
Figure 1. Contents of abscisic acid (ABA; upper panel) and cytokinins (zeatin [Z] and zeatin riboside [ZR]; lower panel) in embryos, maternal pericarp, and mature foliar tissues of 10 viviparous mangrove species (gray bars) and four nonviviparous, upland species (white bars). Means across species ($N = 9$ [three samples of three propagules per age or leaves per species]) ±1 SE are shown. Cytokinins and ABA were quantified using methods of Farrant et al. (1993). Viviparous species were *Bruguiera exaristata* Ding Hou, *B. gymnorrhiza* (L.) Lamk., *Ceriops decandra* (Griff.) Ding Hou, *C. tagal* (Perr.) C. B. Robinson, *Kandelia candel* (L.) Druce, *Rhizophora mangle* L., *R. stylosa* Griff., *Aegiceras corniculatum* (L.) Blanco, *Nypa fruticans* (Thunb.) Wurmb., and *Aegialitis annulata* R. Brown. Nonviviparous species were *Cassipourea elliptica* (Sw.) Poir., *Ardisia escallonioides* Schiede & Deppe, *Limonium perigrinum* (Berg.) R. A. Dyer, and *Phoenix reclinata* (Jacq.). Members of the mangrove Rhizophoraceae (*Bruguiera*, *Rhizophora*, *Ceriops*, and *Kandelia*) showed high interspecific variation in cytokinin levels; thus, incorporating a correction for phylogenetic relatedness by pooling data across the Rhizophoraceae did not change the results. An asterisk indicates a significant difference ($P < 0.05$ by ANOVA within tissue type and age, comparing family means) between viviparous and nonviviparous species.

during developmental “competence” windows that reflect ontogenetic adjustments in hormone production and sensitivity. Disparities between levels of ABA among different tissues indicate tight control and early maternal effects on localized deployment of this phytohormone in these plants.

It is of interest that such compartmentalization has apparently occurred multiple times during the independent evolution of mangrove lineages, and that low ABA levels and consequent precocious germination characterize many species of flooded and saline sites (Farnsworth 2000). The evolutionary reasons for this convergent switch are not entirely clear, although Elmqvist and Cox (1996) posit plausibly that once such vivipary arises, the phenotype may enjoy a selective advantage in heterogeneous environments where suitable sites for germination and establishment may be few and far between. More studies of hormonal change in a phylogenetic context become feasible as our understanding of evolutionary relationships improves. Clearly, selection pressures act differently on young and mature phases. Do low levels of ABA in mangrove seeds, for example, permit the rapid growth of the embryo even under highly saline conditions experienced by the maternal tree? Do comparatively high levels of ABA in adult foliar and root tissue enable the mature tree to maintain the conservative photosynthetic and growth rates typical of mangroves (Ball 1988, Farnsworth and Ellison 1996)?
Fig. 2. Contents of free ABA (upper panel) and cytokinins (Z and ZR; lower panel) in propagules of Rhizophora mangle subjected to osmotic manipulation while still on the parent tree. Bars show mean values (±1 SE) for three samples of 10 propagules per treatment. ANOVA with post-hoc Schef- fe test was performed (N = 10 propagules per treatment, df = 3). ABA levels were significantly different (P < 0.001) only in the freshwater injection, which altered salt contents of embryonic tissue relative to the other three treatments. Cytokinin levels were significantly lower (P < 0.01) in the saltwater- and freshwater-injection treatments relative to the two control treatments.

Field studies indicate that ABA may figure in slowing leaf growth (by reducing cell wall extensibility) and photosynthesis, especially in species with long leaf lifespans in osmotically challenging environments. Evergreen and semideciduous tree species show higher xylem ABA levels during the dry season of the Australian savannah than do deciduous species (Thomas and Eamus 2002). Mangroves, with high foliar ABA levels, exhibit long leaf lifespans (estimated range across 13 species is 9–42 mo) relative to upland evergreen tropical trees (summarized by Ellison and Farnsworth 1996). Similarly, net photosynthesis remains conservative (essentially flat) across a range of leaf longevities in mangroves, causing the allometric relationship between \( A_{\text{max}} \) (light-saturated rate of net \( CO_2 \) assimilation) and leaf lifespan to depart significantly from that established by Reich et al. (1999) for 105 upland plant species (Ellison 2002). Maximal photosynthetic rates for Rhizophora mangle are highest and most variable among light environments in seedlings; responsiveness of \( A_{\text{max}} \) to light is lower in saplings and declines still further in mature trees (Farnsworth and Ellison 1996). ABA may be implicated in this ontogenetic shift, as saplings and mature trees increasingly utilize this hormone.

In the short term, however, leaf senescence and translocation of scarce internal resources by some plant species can be accelerated by ABA spikes in response to pulses of stress, especially during reproduction (Yang et al. 2002). This mechanism may partially explain why mangroves defoliate when exposed to freezing temperatures, especially if ABA upregulation is not accompanied by increased chaperonin protein production (Farrant et al. 1996). The interaction between multiple stressors on hormone regulation merits more exploration.

Cytokinins, seeds to senescence.—Cytokinins, common adenine derivatives, promote cell growth and division (Thimann 1987). The four naturally occurring, physiologically active, cytokinin compounds are zeatin (Z), zeatin riboside (ZR), dihydrozeatin, and isopentenyl adenine (IPA). The considerable challenges of developing nonlethal mutants (Miklashevichs and Walden 1997) have hindered progress in understanding cytokinin signal transduction, but recent work has begun to overcome these limitations (Vogel et al. 1998, Hutchison and Kieber 2002). Genetic studies indicate that these pathways are complex, redundant, and interactive with other hormonal pathways (Schmülling et al. 1997, D’Agostino and Kieber 1999). Cytokinins accumulate in actively dividing meristems, and are most abundant in plant compartments that are rapidly growing, such as elongating stems of germinating seedlings, proliferating roots, and nondormant embryos. They accrue early in the growing season in vegetative tissues, attain high levels in young plants, and decline in mature, fruiting individuals (Mercier and Endres 1999). The types of cytokinins produced—IPA-type vs. Z-type—can be indicators of particular maturation phases (Valdes et al. 2002). Sensitivity to cytokinins also changes as plants age and cope with new stressors such as salinity (Amzallag 2001, Yang et al. 2002). Cytokinins regulate vascular tissue differentiation (Ye 2002) and, acting in opposition to auxin, overcome apical dominance to promote the formation of lateral buds (Emery et al. 1998, Cowan et al. 1999).
Cytokininns increase cell wall plasticity and protect cell membranes by inhibiting formation of and hastening breakdown of free radicals (Thompson et al. 1987). Cytokinins also delay leaf senescence (e.g., Jordi et al. 2000), both by reducing free radicals and by heightening the capacity of plant tissues to act as sinks for phloem transport of sugars and nutrients (principally N). Cytokininns promote photosynthesis by upregulating production of two important photosynthetic proteins: the small subunit of rubisco (rbcS) and the major chlorophyll a/b-binding polypeptide of the light-harvesting complex in chloroplasts. They also appear to stimulate plant growth under high light by way of additive and independent pathways from phytochrome (Fankhauser 2002). In promoting growth and photosynthesis and creating nitrogen sinks in sun leaves relative to shaded leaves, cytokininns also function in light sensing and allocation under a canopy (Pons et al. 2001).

Cytokinins also figure importantly in the formation of plant mutualisms with symbiotic bacteria and mycorrhizae. Cytokinin production by symbionts stimulates promoter activity of nodulation genes and facilitates nutrient transfer between the plant and its partner (Ng et al. 1982).

In seeds, cytokinin levels usually peak during early histodifferentiation, when the embryo is undergoing rapid cell division. In nondormant seeds produced by viviparous mangroves and recalcitrant species, for example, cytokininns peak in early and intermediate developmental stages (Fig. 1, Fig. 3, and Farrant et al. 1993); however, mangrove species show only marginally to significantly higher levels of cytokininns (Z and ZR) in young and intermediate-aged embryos and maternal (pericarp) tissues relative to related non-mangroves (Fig. 1). Variance among viviparous taxa suggests that these differences may be more reflective of responses to osmotic stress than to the evolution of viviparity per se. Rather, cytokininns may be linked with the import of sugars (which act as compatible solutes) into embryonic cells. For example, cytokinin concentrations dropped in the experimentally manipulated R. mangle propagules described above, most precipitously in those injected with fresh water (Box 1, Fig. 2). Similarly, mangrove propagules from the low-salinity riverine site showed the lowest levels of cytokininns of the three populations studied throughout ontogeny (Box 2, Fig. 3), while the youngest propagules from the hypersaline site showed high concentrations.

ABA and cytokininns have long been regarded as antagonists, showing opposing effects on cell division, resource allocation, and stress reactions and interference in each other’s synthetic pathways (Jacqmard et al. 1995, Cowan et al. 1999, Wilkinson and Davies 2002). ABA counteracts cytokinin-dependent activities of several genes, including those involved with transcription of photosynthetic proteins, transitions between C₄ and C₃ photosynthesis, and responses to salt stress (Schmülling et al. 1997). When ABA levels are high in tissues, cytokinin levels tend to be low, and vice versa. Such is the case for the seeds studied here (Box 1, Fig. 1, Fig. 3). However, an exception exists in mangrove leaves, where both cytokininns and ABA concentrations are higher relative to non-mangrove species (Fig. 1) and may be able to coexist in different cellular compartments. As cytokininns delay leaf senescence, they could be implicated in the very long life-
Fig. 4. Conceptual model linking actions of ABA, cytokinins, and their cofactors (calcium and sugars, respectively) to environmental responsiveness, development, and fitness. Arrows indicate a positive (black) or negative (white) effect of hormones on a given process; dotted lines indicate a temporal as well as physiological link between processes. Processes are arrayed vertically according to the time scale over which they occur.

span of mangrove leaves. Indeed, measured Z and ZR concentrations in leaves of five mangrove species correlates positively with leaf lifespan ($r^2 = 0.954$, linear regression of leaf lifespan on measured mean Z and ZR levels; Ellison 2002; unpublished data). However, this correlative link needs to be explored in more detail with experimental and comparative work.

DISCUSSION

Although measurement of hormone levels in plants is highly suggestive of the roles they may play in the autecology of plants, the story of hormone action is a complicated one. Data on levels by themselves tend to be correlative and should be interpreted with caution. Quantifying levels alone will contribute to new hypotheses, but will not be sufficient in the long run to elucidate hormone roles. Thus, plant ecologists and physiologists must collaborate both to understand hormonal pathways fully and to comprehend the ecological significance of molecular studies. Weyers and Paterson (2001) aptly review the history of hormone concepts and caution that simple dose–response relationships do not always hold because of lags, feedbacks, differing rates of anabolism and catabolism in synthetic pathways, complex actions of cofactors (such as calcium), differing sensitivities among plant tissues, and the interaction of stimuli and hormones in inducing signal cascades. The early data from field studies reviewed here must be accompanied by controlled experiments that demonstrate: replicable correlations of hormones with responses; deletion and reinstatement of hormone action; specificity; isolation of biochemical responses from confounding factors; distinguishable roles of de novo production vs. translocation and activation of compartmentalized hormones; relevance to actual performance of plant phenotypes in the field; and generality among species.

Chapin (1991) developed a cohesive model by which ABA serves to reduce photosynthesis, stomatal conductance, and plant relative growth rate in conditions of drought, flooding, and low nitrogen availability. Later, this model was extended to encompass ABA and cytokinins (Chapin et al. 1993). In a similar vein, Leshem and Kuiper (1996) proposed a hypothetical “general adaptation syndrome” for plants, which incorporates new understanding about signal transduction pathways, chaperonin proteins, and other phytohormones. Most recently, ubiquitous and evolutionarily
conserved heat shock proteins have been found to modulate both short-term responses to stress and to stabilize development of the phenotype as a whole in both plants and animals (Queitsch et al. 2002). Subsequent experimental work has contradicted certain elements of Chapin’s findings, which may reflect the complexity of hormone action discussed above and points to the need for testing these hypotheses (Coleman and Schneider 1996).

Together, this new information and findings from comparative studies allow us to elaborate on the Chapin et al. (1993) model, incorporating a sense of both changing selection pressures and shifting hormone action over time, encompassing both temporary acclimation and longer-term ontogeny (Fig. 4). This model can ultimately incorporate synergistic effects of multiple hormones, cofactors, and environmental drivers to provide more mechanistic explanations of plant behavior, linked traits, and evolution. For example, as experiments elucidate the influence of multiple stressors, such as competition, on the costs and benefits of inducible defenses (e.g., Van Dam and Baldwin 2001, Cipollini 2002) and light responsiveness (Donohue and Schmitt 1999, Weig and Delph 2001), it is becoming clearer that phytohormones can help explain mechanisms of plasticity in complex environments. A better understanding of hormones may clarify several life history conundrums, which, to date, have been received more attention in animals than in plants (Ricklefs and Wikelski 2002). For example, how do life history constraints arise; do hormonal mechanisms permit only certain combinations of physiological and architectural states to occur in plants? Are correlated traits (such as reduced seed dormancy, conservative photosynthesis, longer leaf life spans, and salt tolerance) linked through the pleiotropic (sensu McCourt 1999) nature of genes that control hormones and their tissue-specific effects? Age-specific studies of hormones may also help identify “constraints of resource harvesting and biomechanics on plant growth and development” (Enquist et al. 1999:908) that shape the allometry of basic plant traits as they grow.

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LITERATURE CITED


